SORGHUM PACHYTENE KARYOTYPES[1]

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ABSTRACT

Sorghum [S. *bicolor* (L.) Moench] pachytene chromosomes show considerable detail in morphology. Previous reports have characterized karyotypes. In the present study, karyological observations covered a wide range of sorghum germplasm. Most collections were found unsatisfactory for karyotype analysis. Of those which were satisfactory, exhaustive simultaneous comparisons of chromosome lengths, arm ratios, and other morphology could not establish any complete karyotypes. Of the ten chromosome pairs, however, one nucleolar pair and one asymmetric pair were easily identified. A group of three longer pairs could be distinguished from five shorter pairs. Beyond this, it did not seem that complete karyotypes could ever be obtained, in view of the large length variation computed for the two identifiable chromosomes. This variation could not be entirely assigned to hypotheses of chromosome shortening or to any feature of the technique, though each step of the technique was analyzed for its reliability. The nonconformity of the present results from those of previous reports challenges the repeatability of the previous experiments. This, in line with statements by some sorghum workers, suggests that the basic karyology of sorghum is not well understood.

Sorghum bicolor (L.) Moench (Gramineae) includes the grain sorghums, cultivated widely in many of the world's developing regions—in much of Africa, and parts of India and China. Sorghum is thereby one of the six great staples in the human diet along with rice, wheat, cassava, maize, and the potato (Brown, 1963: 32).

I can think of two general purposes that speak for the application of cytology to cultivated plants. The first of these purposes is crop improvement; the second is the synthesis of new knowledge. One outgrowth of modern plant breeding has been the search for ways of applying cytology to selecting better crop varieties. Basic information on the chromosomes and their behavior has been sought for the major crops of the world. Admittedly, much of this information is yet to be of wide use. But the recent field of cytogenetics has provided the bases for the substitution of alien germplasm, techniques using autoploidization, and means of manipulating breeding systems to do much of the work of selection. These new tools already promise some amelioration of human life, in the face of expanding populations.

A further development of cytology in its application to cultivated plants is indirect knowledge of crop variation and origins. Anderson (1952: 72) said, "But quite as important as any of the specific information which it [cytology] contributes to the problem of the origin of cotton or the origin of tobacco, is the

[1] Derived from portions of a thesis submitted to the Graduate College of the University of Illinois in partial fulfillment of the requirements for the degree of Master of Science in Agronomy. Made possible by a Graduate Research Assistantship in Crop Science from the Agronomy Department of the University of Illinois Agricultural Experiment Station. I sincerely thank Mrs. Betty C. Busey, for making most of the pachytene chromosome measurements used in this study, and Dr. Jack R. Harlan, for encouragement and suggestions during the compilation of the observations. All collections were obtained from the herbarium of the Crop Evolution Laboratory of the Agronomy Department of the University of Illinois.

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ANN. MISSOURI BOT. GARD. 58: 245–257.

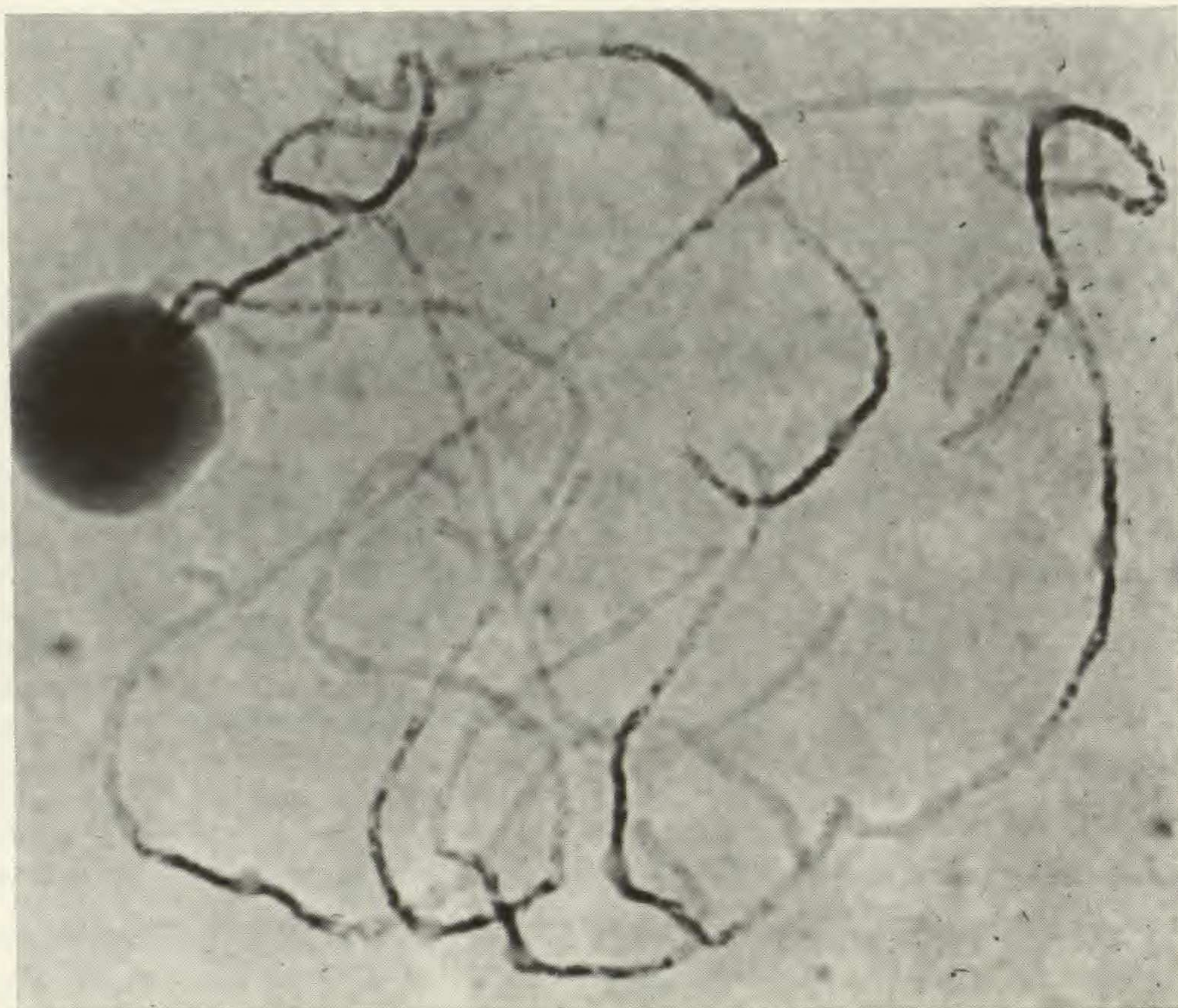

FIGURE 1. Pachytene chromosomes of *Sorghum bicolor* with 10 pairs separable (accession 2399), 1870 ×.

bearing of cytological evidence on the general problem of cultivated plants as a whole."

This "general problem" is one which has synthesized many fields and brought about new knowledge of man and his universe. Darwin (1868: 18) was one of the first to be aware of the ecological and evolutionary implications of domestication—"no limit exists to the number, singularity, and perfection of the contrivances and co-adaptations which may . . . be produced. An animal or a plant may thus slowly become related in its structure and habits in the most intricate manner to many other animals and plants, and to the physical conditions of its home." Other fields allied around the study of domestication include cytology, archeology, taxonomy, and history. With the new knowledge of domestication man may be seen as a connecting piece in the web of life; as a symbiote, he may be further comprehended in terms of the tie between his cultural evolution and the hereditary changes of his fellow travelers. And an intelligent view of the environment, and the successful use of it in the future, must also depend on the lessons from the past, that is, the history of man's recent biological advances.

For all this, of course, or even a part of it, we must obtain the best possible information. This paper reports a test of previous considerations of sorghum chromosomes—knowledge which has already been used to develop inferences concerning the evolution and genetic nature of S. *bicolor*.

Sorghum pachytene chromosomes show considerable detail, in the form of easily distinguishable centromeres and differentiation into dark- and light-staining regions (Fig. 1). A number of chromomeres of various sizes can often be

distinguished near the margins of the median dark-staining regions. There is variation in the pachytene arm ratios, and one and only one chromosome pair (the longest of the complement) is consistently associated with the nucleolus.

Previous reports (Magoon & Ramanna, 1961; Magoon & Shambulingappa, 1960, 1961; Magoon, Shambulingappa & Ramanna, 1961; Venkateswarlu & Reddi, 1956, 1968) have established karyotypes for thirteen collections within the complex *S. bicolor.*[3] Reddi (1970*b*) has extended karyology to a $2n = 40$ *S. bicolor* and (1970*a*) to two other collections, one of which must also be classified as a $2n = 40$ *S. bicolor.*

A wide range of sorghum germplasm was available to me. This included types with wild, weedy, and cultivated adaptations, several of which were from remote regions of Africa. It was hoped that a study of pachytene in these materials, as well as several artificial hybrids, would help further characterize variation patterns in the group.

Materials and Methods

The materials studied (Table 1) were field grown from seed accessions or were field-grown hybrids. Inflorescences in the flag-leaf stage were collected from one plant for each material and fixed in 3:1 95% alcohol–acetic acid or in 3:1 absolute alcohol–propionic acid. No difference in the results from these two fixatives was noted. After at least 18 hours, the inflorescences were transferred to 70% alcohol and were stored in a refrigerator. Due to the attenuated nature of the pachytene chromatin, a more intense and yet standardized staining method was used than what is satisfactory for diakinesis-metaphase studies. Thus a system of mordanting the sporocyte tissue before staining (Swaminathan, Magoon & Mehra, 1954) was used successfully. Therein the propionic acid of the fixative is saturated with ferric acetate. Previously fixed materials were also successfully mordanted by placing them in such a mordant-fixative solution.

Meiotic anthers were stained and squashed in the standard way, except that a small steam bath was used in warming them. Barton (1950) suggested this procedure to avoid the violent heating of an alcohol lamp.

Good quality cells at pachytene were selected and their chromosomes were traced with a camera lucida apparatus. All cells were photographed before their slides were made permanent. Photographs were taken using an oil-emersion objective (100 ×/1.3 apertures) with a film holder set-up, such that the final magnification was 1870 ×.

Measurements of the pachytene chromosomes were made from hand-traced 5 × enlargements of the photographs. Separate measurements were made of each arm and of the total length for each traceable chromosome pair. Camera lucida drawings were not used for any measurements, but rather to solve problems of chromosome overlaps which could not be resolved from photographs.

A total of 329 fully traceable pachytene chromosomes were measured, in 79 cells of 6 accessions (1015, 1539, 1553, 1581, 1937, and 2399) and one artificial hybrid (S-69X-6). Of these, 17 cells were fully analyzable (each of the ten chromosome pairs could be traced from end to end). Another 9 cells were not fully analyzable, but in the latter the total chromosome length per cell was measured by pooling the segments of the chromosomes which could not be individually separated. Three accessions, 1539, 1581, and 2399, were particularly useful, based on the number of analyzable cells obtained from them, and the measurements of their chromosomes were submitted to several statistical analyses. The collections from which no fully traceable pachytene chromosomes were obtained were useful in studying qualitative variations.

Arm ratios were calculated by dividing the length of the short arm by that of the long arm,

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[3] *Sorghum bicolor* includes diverse wild, weedy, and cultivated forms indigenous to all but the driest regions of Africa, and now found in every major habitable region of the world. Although once classified into 49 species (Snowden, 1936, 1955) the group is not recognized to have broad fertility barriers, discrete morphological isolates, or naturally occurring cytotypes. Therefore the conspecific treatment of this complex is used here to describe all $2n = 20$ forms within the section *Sorghum.*

TABLE 1. List of *Sorghum bicolor* materials studied. All materials were obtained from the Crop Evolution Laboratory of the Agronomy Department of the University of Illinois.

ORIGINAL COLLECTIONS

Accession number	Origin	Collector	Race[a]	Adaptation
1014	Guinea, Butu	Unknown	Arundinaceum	Wild
1015[b]	Rhodesia, Salisbury	Unknown	Bicolor	Cultivated
1016	South Africa, Kimberley	Unknown	Verticilliflorum	Wild
1018	Egypt, Cairo	*ex* U.S.S.R.	Virgatum	Weedy
1452	Java, Bogor	Unknown	Bicolor	Cultivated
1539[b]	Sudan, El Obeid	Harlan	Guinea-caudatum	Cultivated
1541	Sudan, El Obeid	Harlan	Guinea-caudatum	Cultivated
1553[b]	Sudan, Nuba Mountains	Harlan	Caudatum	Cultivated
1581[b]	Chad, Fort Lamy	Harlan	Caudatum	Cultivated
1930	South-West Africa, Okahandja	de Wet	Bicolor	Cultivated
1937[b]	South-West Africa, Omatoka River	de Wet	Verticilliflorum	Wild
2080	South Africa, Lobatsi	de Wet	Kafir	Cultivated
2399[b]	Sudan, Simsim	Harlan	Shattercane	Weedy
2577	Ethiopia, Awash	Harlan	Verticilliflorum	Wild

ARTIFICIAL HYBRIDS[c]

Number	Parents	Racial designation of parents
S-68X-24	1015 × 1021	Bicolor × Shattercane
S-68X-27	1015 × 1014	Bicolor × Arundinaceum
S-68X-31	1021 × 1020	Shattercane × Shattercane
S-69X-6[b]	1016 × 1452	Verticilliflorum × Bicolor
S-69X-7	1026 × 1018	Aethiopicum × Virgatum
S-69X-12	1016 × (1014 × 1016)	Verticilliflorum × (Arundinaceum × Verticilliflorum)

[a] Racial designations are based on a descriptive classification of variation within S. *bicolor*. See pp. 2–4 *in* P. Busey, "Meiosis and karyotypes in *Sorghum bicolor* (L.) Moench." M.S. thesis, University of Illinois.

[b] These seven materials were used for pachytene chromosome measurements.

[c] The artificial hybrids were made by E. G. Price.

thus giving values not greater than 1.0. Relative lengths were also computed, and these are a percentage of the sum of the chromosome lengths in the cell. In the statistical analyses, the figure "±" following a number indicates the standard deviation. "N" represents the sample size, in contrast to "*n*," the haploid number of chromosomes.

RESULTS AND DISCUSSION

Only seven of the twenty accessions or hybrids were found suitable for pachytene chromosome measurements. The determining factor lay in the completeness of separation between chromosome pairs. It is necessary to discuss some of the theory which must go into karyotype comparisons.

It is assumed that there is a degree of consistency in chromosome characteristics between different pachytene cells of the same material. An intensive study of the chromosomes should reveal repeatable defining patterns, called the "karyotype." A reasonable approach accepts that cell-to-cell differences are superimposed on differences between chromosomes. Thus in the intensive comparisons, cellular variations must be accounted for. The procedure here was to consider relative lengths for each chromosome (as a proportion of the sum of the chromo-

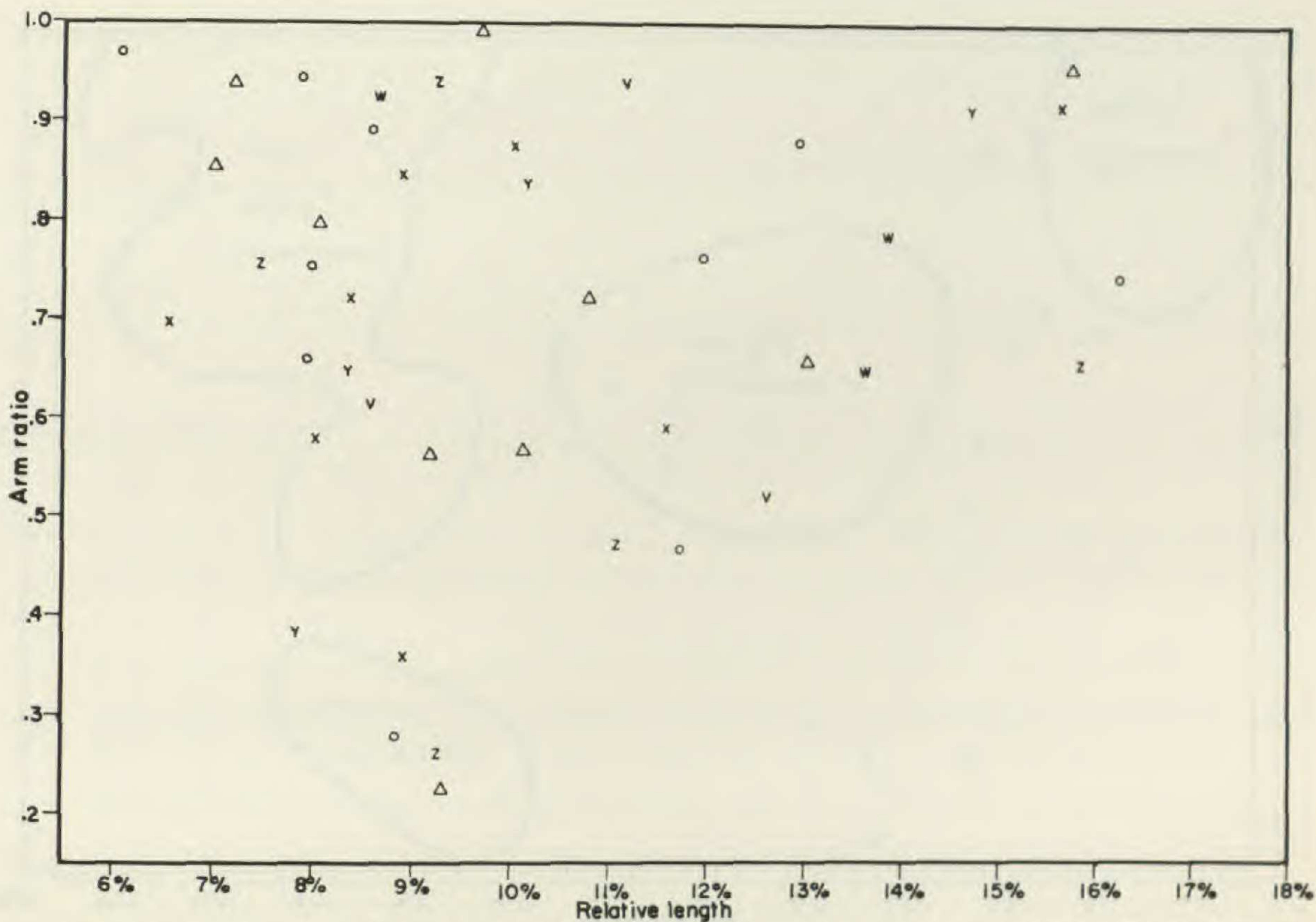

FIGURE 2. A plot of the chromosome measurements from accession 1539. Each different symbol locates the chromosomes in a single cell. Letter symbols refer to cells which were not fully analyzable.

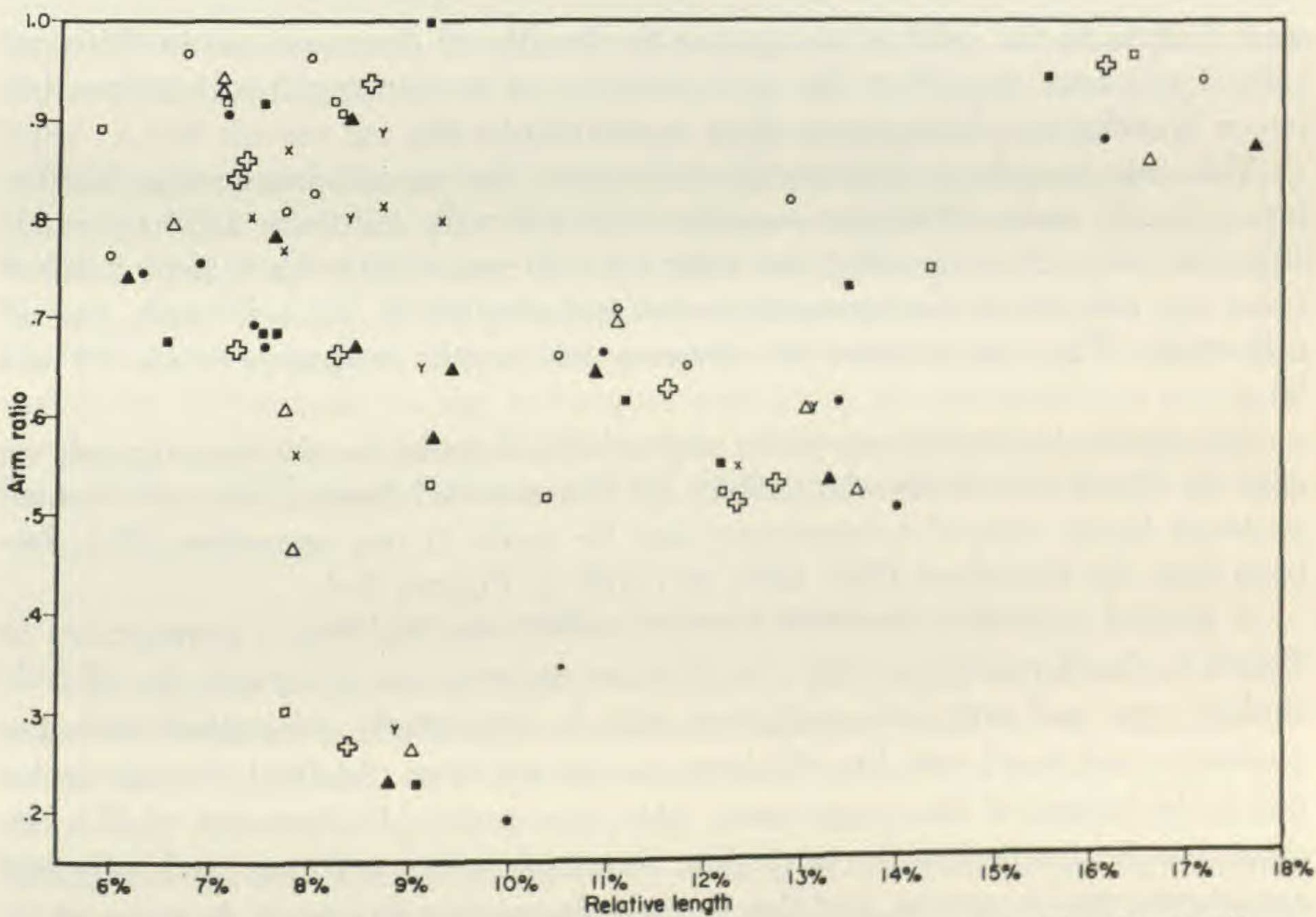

FIGURE 3. A plot of the chromosome measurements from accession 1581. Each different symbol locates the chromosomes in a single cell. Letter symbols refer to cells which were not fully analyzable.

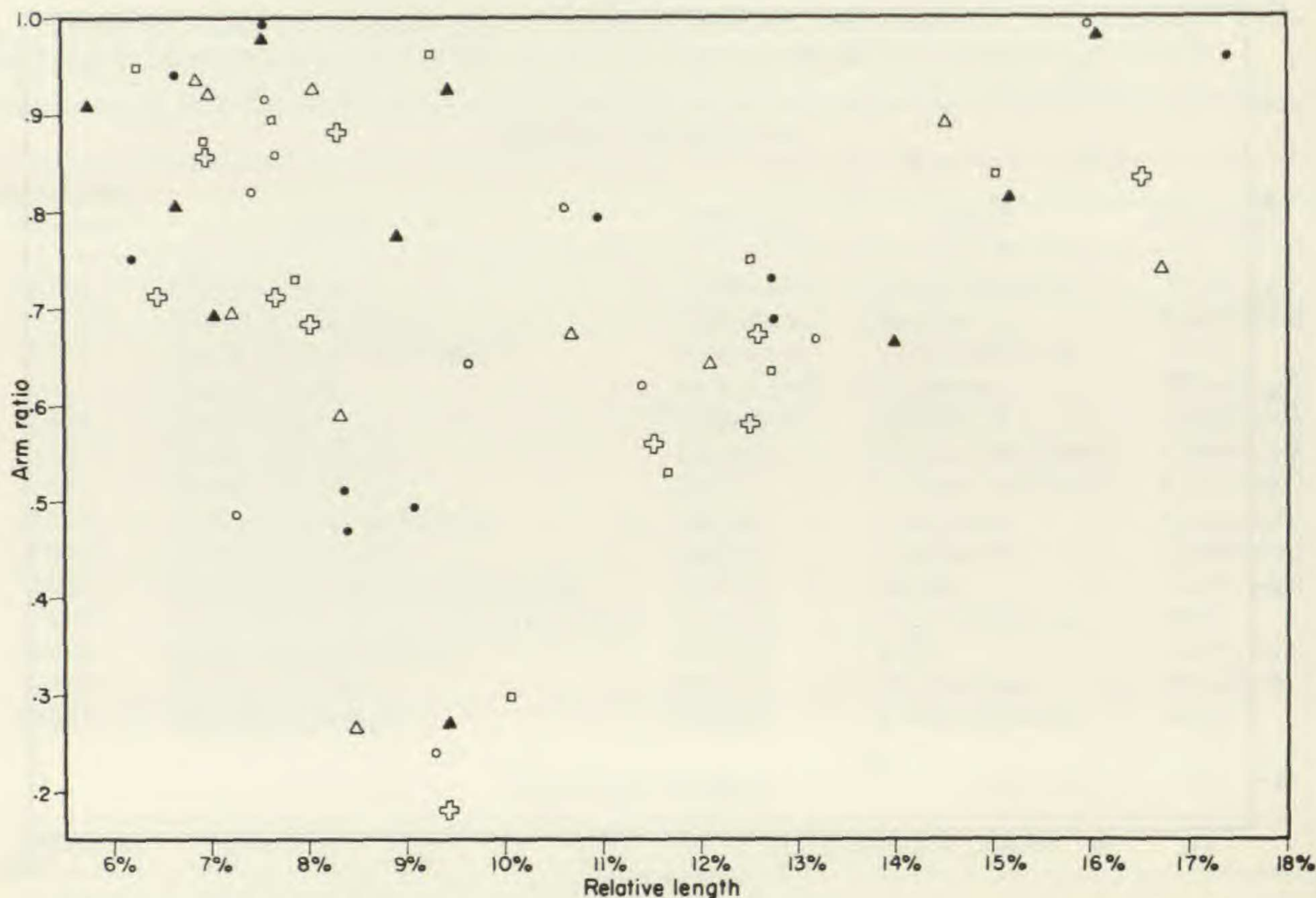

FIGURE 4. A plot of the chromosome measurements from accession 2399. Each different symbol locates the chromosomes in a single cell.

some lengths in the cell) in comparing the lengths of chromosomes in different cells. I will later show that this was a useful tool in reducing the variations between homologous chromosome pairs in different cells.

The mean lengths, in microns, for cell totals (the sum of chromosome lengths for each cell) were: 389.3 for accession 1539 (N = 7); 350.0 for 1553 (N = 3); 323.1 for 1581 (N = 9); 475.8 for 2399 (N = 6); and 340.5 for hybrid S-69X-6 (N = 1). Individual chromosomes varied from 6–18% of the cell totals, for all collections. The actual values for chromosome lengths ranged between 15 and 90 μ.

By means of plotting arm ratios and relative lengths on the same graph, as used by Essad and Najcevska (1969) for the mitotic chromosomes of *Festuca pratensis* Huds., several comparisons may be made in one operation. This has been done for accessions 1539, 1581, and 2399 in Figures 2–4.

A general pattern is consistent between collections, and this is summarized in Figure 5. In all pachytene cells ten chromosome pairs are observed. In all cells studied, one and only one pachytene pair is consistently associated with the nucleolus, and in all cells for which measurements were obtained, this nucleolar pair is the longest of the complement. Most commonly (18 times out of 25), the short arm is attached to the nucleolus. In nearly every cell, one and only one asymmetric pair is present, and this is regularly number five or six in terms of its rank—based on length—with the other pairs in the cell. In each material for which pachytene measurements were obtained, there is a clear indication that

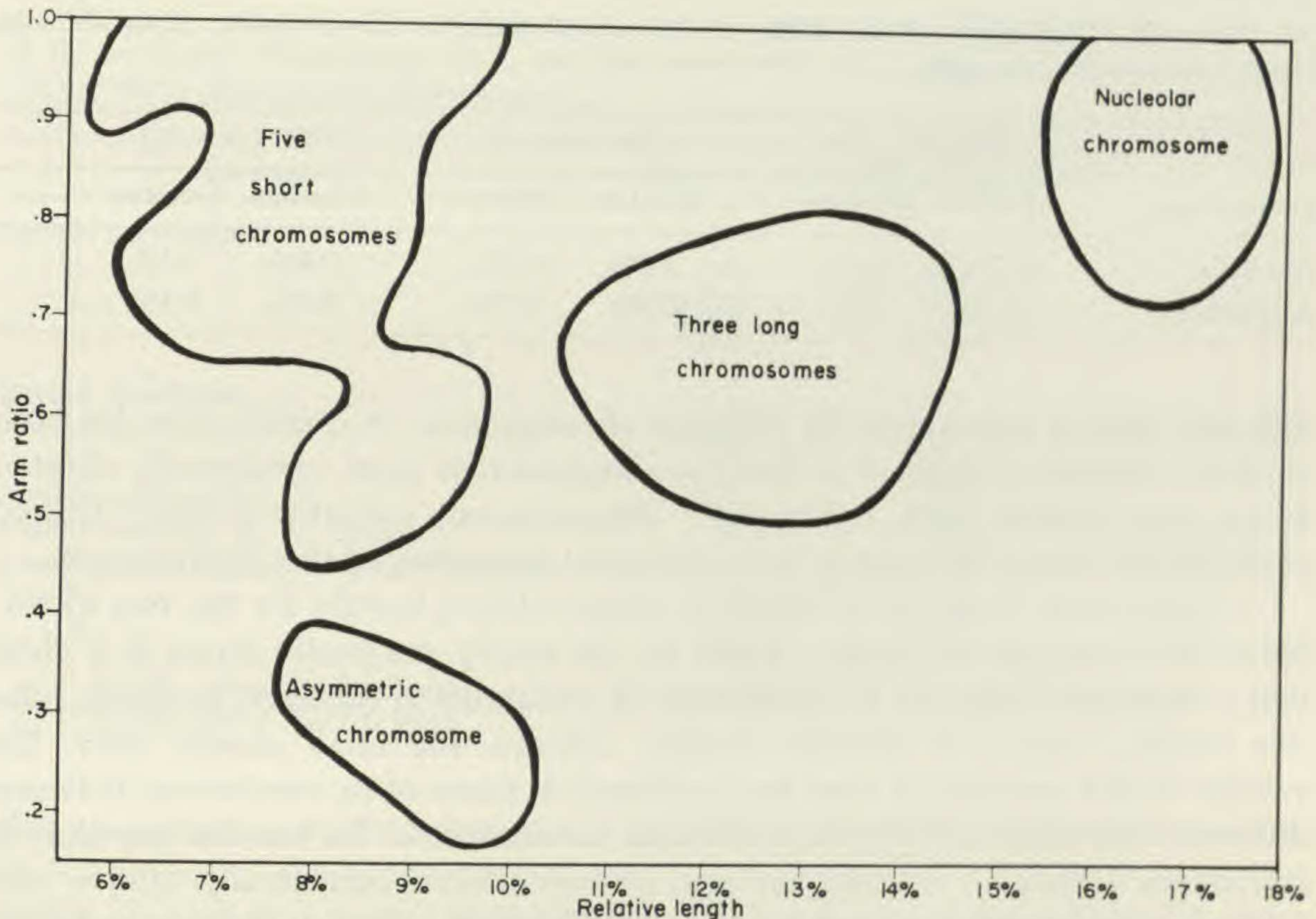

FIGURE 5. A plot summarizing the chromosome measurements from accessions 1539, 1581, and 2399. Of 185 chromosomes 90.3% fit within the distributions shown.

three relatively long and five shorter pairs are definable. It seems that finer distinctions than these cannot be established, to say nothing of complete karyotypes. I will devote the rest of this paper to discussing this conclusion.

Exhaustive comparisons had been made between chromosomes. In addition to comparisons based on arm ratios and relative lengths, absolute lengths were worked with, and variations in morphology (dark-staining regions and chromomeres) were studied. Many possible homologies were observed, but too many contradictions appeared to establish complete karyotypes. It was realized that variability attributable to the techniques and/or to the chromosomes could be present. In addition, the size of the sample could have been too small, though for accession 1581 it involved seven fully analyzable cells and a total of 82 individual chromosomes.

ANALYSIS OF CHROMOSOME LENGTH VARIATION

The suggestion (Maguire, 1962) that most of the length variation in homologous chromosomes is attributable to cellular variation (and not to variation between slides or plants), and that this variation is based on a pattern of uniform shortening differences between cells, had been accepted. Uniform shortening differences are here defined as the effect of an equal shortening per chromosome length throughout the complement. This variation would be totally eliminated by the use of relative chromosome lengths to compare homologs in different cells. Continuous-but-nonuniform shortening variation could also exist, being based on

TABLE 2. Coefficients of variability of the two identifiable chromosomes, using absolute lengths *versus* relative lengths.

Chromosome	1539 (N = 4)		1581 (N = 6)		2399 (N = 5)	
	Absolute	Relative	Absolute	Relative	Absolute	Relative
Nucleolar	12.7%	4.2%	5.6%	4.4%	9.6%	4.1%
Asymmetric	12.1%	7.2%	10.0%	8.6%	6.8%	6.1%

different rates of contraction for different chromosomes. A qualification for both of these shortening patterns is that the chromosomes must consistently shorten in the same pattern from cell to cell. Discontinuous variation is here defined as that which cannot be related to a systematic shortening of the chromosomes.

A comparison of the use of absolute *versus* relative lengths for the two identifiable chromosomes was made (Table 2). In purely pragmatic terms it is clear that a fractional reduction in coefficients of variability is obtained by using relative lengths instead of absolute lengths. Despite the small sample sizes, the validity of this comparison must be considered in terms of its consistency between different collections and between different chromosomes. To test the question of continuous variation (whether uniform or nonuniform) statistically, simple and multiple correlation tests were performed (Table 3). For multiple correlation, the absolute lengths of the two identified chromosomes of accession 1581 were compared to the total absolute lengths of the eight unidentified chromosomes. The lengths from accession 1539 and 2399 were treated similarly, but by a means which pooled their variances to give a combined sample 1539-2399. (Pooling was justified because the total variances for 1539 and 2399 were similar.)

Based on the determinable variation, from multiple correlation of the two identified chromosomes with the sum of the eight unidentified chromosomes, the non-determined, or unaccountable, variation of the two identified chromosomes can be estimated. This is shown in Table 3, and the weighted averages of coefficients of variability are 4.58% for the nucleolar chromosome, and 7.92% for the asymmetric chromosome. (These values reflect standard deviations per chromosome of 3.09 μ and 3.00 μ, respectively.) These values are our best estimates of chromosome length variation not determinable by a continuous, linear shortening process, whether or not that shortening was uniform for different chromosomes.[4] This non-determined variation is, according to our definitions, discontinuous. If this non-determined variation were present in a similar magnitude in the eight unidentified chromosomes, it could seriously hamper karyotype analysis.

ANALYSIS OF TECHNIQUE

Because a non-determined chromosome length variation seems to have hampered karyotype analysis, it is important to decide whether the major source of

[4] Curvilinear shortening might at first seem plausible, but it must be remembered that linearity or curvilinearity pertains here not to any absolute standard, such as time, but rather to the comparisons of shortening between chromosomes. Furthermore, it becomes less likely that curvilinear effects would manifest themselves as a variation for samples of this size.

TABLE 3. Statistics from simple correlation, and from the multiple correlation of lengths of the nucleolar chromosome (X_1), and the asymmetric chromosome (X_2) against the sum (X_3) of the 8 unidentified chromosomes.

Parameter	1581 (N = 6)	1539-2399 (N = 9)	
Simple correlation			
$r_{1 \cdot 2}$	.170	.690[a]	
$r_{1 \cdot 3}$	.545	.897[b]	
$r_{2 \cdot 3}$	.272	.731[a]	
Partial correlation			
$r_{31 \cdot 2}$	.525	.794[a]	
$r_{32 \cdot 1}$	.217	.349	
Multiple correlation, R	.574	.910[b]	
Determinability of X_3 variation	33.0%	82.8%	Weighted
Coefficient of non-determined variability			average
X_1	3.86%	4.66%	4.58%
X_2	8.82%	7.41%	7.92%

[a] Significant at the 5% level.
[b] Significant at the 1% level.

this variation was in the technique. I will discuss the technique from five angles: 1) Variations in measurements from the photographs, 2) variations from photography, 3) variation in the vertical placement of chromosomes within the slides, 4) random variations between slides, and 5) uniform variations related to preparation.

The chromosomes from two photographs of the same cell were each drawn and measured twice, on different days. In this replicated experiment, a standard deviation of .33 μ per chromosome was obtained (with 20 degrees of freedom). This cannot account for more than 3% of the unaccountable variance of either accession 1581 or accessions 1539-2399 combined. This estimated measurement variance includes variation in identifying the chromosome ends, in tracing out the 5 × enlargements, and in the use of the map measurer. It does not include mistakes due to the improper solution of overlapping chromosomes. These mistakes were definitely reduced by the use of camera lucida drawings for the direct solution of overlaps and are probably best represented by the 9.7% scatter of chromosomes not fitting the general distribution pattern (Fig. 5). That improper solutions were of little importance is shown by the fact that the two identified chromosomes maintained their approximate ranks with the other chromosomes of the cells.

The optical steps were expectably precise. Photographs of a ruled grid showed no measurable distortions, even when enlarged in the regular manner. The same microscope setting was consistently used, in order to obtain the same magnification. Photographs of a ruled grid were taken on seven different occasions, at an exact same setting as had been used for photographing pachytene cells. The results show that the magnification produced in the photographs of the cells was $1870.1 \pm 6.5 \times$.

No abrupt variations in plane of focus for the chromosomes were observed. By separate focusings, and the use of a calibrated focusing knob, the region of

sharp focus for all the chromatin in seven cells from a permanent slide was estimated to be 1.23 ± .28 μ. This represents a slight, barely visible slope across the cell; no abrupt, vertical wiggles were seen in the chromosomes. On this basis, no hypothesis of vertical displacements could account for a considerable part of the length variations observed.

Variations probably exist between slides, and these are likely to reflect different stages of contraction in the anthers from which the slides are made. Slide variations should not be a major factor here in the chromosome length variations; out of the fifteen cells which went into these calculations, eleven came from only one slide for each material. Of the four which did not, the cell totals of two of these cells were within the range of cell totals for the principal slide of the material.

Slide preparation was done as cautiously as possible, by methods standard for many meiotic materials, some of which (*e.g.* maize) have been used extensively in karyotype analysis. Barton's steam bath was used, as previously described. Thus in this respect the results from this study would not be expected to differ from those of other studies.

A HYPOTHETICAL MODEL

Let us illustrate some of the concepts used in interpreting chromosome length variations. Consider yourself an observer in an unusual race, analogous to the "shortening of the chromosomes." Each of the ten vehicles (chromosomes) is approaching (shortening toward) a goal. Unfortunately you cannot readily identify more than two vehicles, but you can try to identify the other eight. But all you have to go on is a set of photographs, presumably all from the same race. (If we have presumed wrong, that is, if the chromosomes in different cells do not synchronize their shortening similarly, as though they were repeating the same race, then these vehicles cannot be identified by observation alone.) Your object is to match the vehicles in the photographs by being able to show their position from one photograph to another, relative to the two identifiable vehicles and relative to each other. Now you had hoped that all ten travel at the same rate (uniform shortening). Unfortunately, they do not. Your next hope is that the ten vehicles travel at a continuous speed throughout the race. You do find that this hypothesis can explain, in one case, over 80% of the variation in locations of the two "marked cars," in relation to the other eight. Yet the remaining, "discontinuous" variation is considerable—sufficient, it seems to hamper identification. In other words, the vehicle locations fluctuate too widely, for unexplained reasons, to follow their locations from one photo to another. And far from identifying the "unmarked cars," we are left to explain the cause for discontinuous variation.

Throughout the present study there has been the realization that pachytene chromosomes are in the midst of a process, that of contraction. Could some special aspect of contraction be responsible for this discontinuous length variation? Yes, I suggest, there could be, and it might come out of the coiling hypothesis of the nature of chromomeres. Brown (1949) suggested that the chromomeres of tomato are formed in light-staining regions and move medianly during pachy-

tene. In the present study, the median dark-staining regions often appeared as groups of fused chromomeres. Eventually the entire chromosomes become dark-staining, perhaps through an accumulation of many chromomeres. Thus I suggest that the chromomeres are temporary knots of chromatin, the formation of which permits the chromosomes to contract and become dark-staining. These knots might be expected naturally as differential coilings within the helical, tightly paired chromosomes. If the suggestion were true, then it is quite likely that the formation of these knots of chromatin would involve abrupt, quantum changes of length during chromosome contraction. This would create some variation residual from a linear correlation test, which would be assigned to discontinuous sources.

Conclusion

The results from the present study have not yielded complete karyotypes. This is in contrast to the report by Magoon and Ramanna (1961: 398) that the pachytene chromosomes of sorghum are "capable of easy identification." It is very difficult to resolve this point. Because the earlier workers have not mentioned the several problems encountered in the present study (availability of high-quality material, chromosome overlaps, and chromosome length variation), it is not possible to assess the relative importance of these problems.[5] It is even possible that unreported differences in technique existed.

In the present study at most seven fully analyzable cells were used for one collection (1581), in contrast to the report of ten fully analyzable cells for each of the earlier studies, with the exception of Venkateswarlu and Reddi (1968), who used eight fully analyzable cells, but at least ten representatives of each chromosome. Yet this does not account for the degree of contrast between the present study and the others. For here there has been no indication that certain chromosomes could ever be reliably separated, or that the number and location of chromomeres had any value in separating the unidentified chromosomes.

In addition, other workers have reported difficulties in working with *Sorghum* chromosomes (Garber, 1948; Hanna & Schertz, 1971; Harpstead, Ross & Franzke, 1954; Lin & Ross, 1969; Schertz, 1966, 1970). Admittedly, most of these workers have been studying aberrations, but Hanna and Schertz (1971: 105) say with some sureness, "No satisfactory karyotype analysis is available in sorghum. . . ."

The general need for repeatability in karyotype analysis has been discussed by Torres (1968: 582), "Often, however, karyotypic data and comparisons based on them are largely subjective and non-operational in the sense that the logical steps which yielded the evidence and led to the interpretations are not indicated and therefore are not repeatable." It would be interesting, then, to know from the data of Magoon and Ramanna (1961), who report some statistically significant differences, what manner of variation was observed in the identified chromosomes. Were these variations uniform between different chromosomes, and

[5] Reddi (1970*a*, *b*) did report difficulty in identifying all chromosomes in $2n = 40$ collections of *Sorghum*.

perhaps correlated with a pattern of shortening; how did they relate to the chromomere pattern?

In any case, difficulties in chromosome identification and problems with the repeatability of results seem to seriously limit full realization of the taxonomically great significance of the "pachytene karyomorphological meioty" (expression by Magoon & Ramanna, 1961: 307).

As an afterword, Schertz (1970) has recently made a great advance in sorghum chromosome identification by the development of a complete set of translocation stocks. This accomplishment will permit many of the practical applications which would be obtainable from accurate and repeatable methods for karyotype analysis. Furthermore, we are nearer to a demonstration as to what, if any, feature of the chromosomes of *S. bicolor* hampers their simple measurement.

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